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Invertebrates of the Littoral Zone of Bering Island - Intermediate and Supplementary Hosts of Bird and Mammal Helminths

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The littoral zone is regarded as the first, upper zone of the sea bottom, which is delimited by the lines of maximum low and high tides. It is characterized, as we well know, by the abundance of life and by the exclusive uniqueness of its manifestation. Invertebrates, which inhabit the littoral zone, are extensively consumed by various vertebrate animals which are in one way or another ecologically associated with the sea.

Apart from the fact that invertebrates of the tidal zone provide food for many animals, they serve as the intermediate and supplementary hosts of helminths which at the adult stages parasitize fish, birds and mammals. The larval forms of the helminths, which parasitize the invertebrates themselves, cause their growth rate, abundance and fecundity to diminish. By doing so, they undermine the food resources of a number of commercially important animals.

As indicated by James (1965), the infestation of the digestive gland of *Littorina saxatilis* (Olivi) by trematode larvae causes partial deterioration of the digestive cells of the liver, the disappearance of reserve nutrients from their cytoplasm, and an imbalance in the content of glycogen and glucose in the hemolymph and tissues of the liver. According to the data of V.V. Kuznetsov and G.K. Chubrik (1950), the parthenitae of *Microphallus pygmaeus*, by infesting the sexual gland of *Littorina obtusata* and *L. saxatilis*, can cause total sexual sterility in the mollusks. According to Rausch (1953), *Microphallus pirum*, a parasite of the sea-otter, causes acute enteritis when it becomes localized in the intestine of the host. The development cycle of

this helminth (*M. pirum*) is assisted by the littoral crustacean *Pagurus hirsutiusculus* (Schiller, 1959).

The above facts point to the current biological and practical importance of studying the helminth fauna of marine invertebrates in general, and of littoral ones in particular.

Up to the present time, Soviet scientists have conducted investigations on the parasitic fauna of marine invertebrates in the White and Barents seas (Amosova, 1955; Belopol'skaya, 1953; Zelikman, 1950, 1951, 1953, 1955, 1962; Kulachkova, 1953, 1961; Kuznetsov and Chubrik, 1950; Uspenskaya, 1960, 1963; Chubrik, 1950, 1952, 1954, 1957), the Baltic Sea (Belopol'skaya, 1957), the Black Sea (Dolgikh, 1964, 1964a, 1965, 1965a), and the Caspian Sea (Kurochkin, 1962, 1963; Zablotsky, Kurochkin, Sudarikov, 1964; Sudarikov, Kurochkin, 1964). Many of them have been carried out in the ecological and parasitological aspect, and therefore are of great scientific and practical interest.

The foreign literature contains a large number of papers on the parasites of marine invertebrates, but their [main] subject of study is the parasite itself, which is of interest to the authors either from the biological, or zoological point of view.

Marine invertebrates of the Soviet Far East have not been studied in the aspect of interest to us.

Physicogeographic characteristics of Bering Is.

The largest of the Commander Isls., Bering Is., is washed by the waters of the Pacific Ocean on the southwest, and by the Bering Sea on the northeast.

The coastline of the island is slightly rugged. The bays are small and open, and are distinguished by strong breakers. A branch of the warm Kuroshio Current passes close to its shores. The high tides are of an irregular semi-diurnal and diurnal nature, with a clearly defined diurnal inequality in the levels of the high and low tides. The salinity of the waters in the coastal areas approximate ocean salinity.

The climatic conditions are quite severe. The specific features of the climate are high humidity, extremely strong winds, and very little warmth.

The island abounds in marine vegetation. Overgrowths of sea cabbage (*Laminaria, Alaria*) occur in large natural plantations along the entire coast.

The littoral zone of the island is exceptionally abundant in living organisms. Characterizing the Commander Isls., Ye.F. Gur'yanova (1935) assigns the littoral zone of these islands to the southern, warm-water type, with a luxuriant growth of

algae, with an abundant and diverse fauna and migration of the organisms to the upper parts of the tidal zone which is constantly kept wet by the spray of the surf and the mist.

The reef near the village of Nikol'sky where our investigations were conducted provides favourable conditions for the typical inhabitants of the littoral zone.

The tidal phenomena serve as an important factor of the zonal distributiion of organisms in the littoral zone. According to the standard system of littoral zonation, the littoral zone is divided into three horizons; the upper (1st) one is completely submerged only during the syzygial high tide; the middle (2nd) one lies between the median level of the small quadratural high tide and the median level of the small quadratural low tide; the lower (3rd) horizon is submerged for the greater part of the time, and is exposed only during syzygial low tides.

Observations in the littoral zone of the reef near the village of Nikol'sky have shown that small overgrowths of algae of the genera *Fucus, Ulva, Monostroma, Enteromorpha* and *Rodomela* occur in the tidal zone along the coast. The upper part of the upper horizon is completely devoid of algae. Of the animal organisms, *Orchestia ochotensis* was found in mass abundance here. Algae begin to appear in the littoral zone from the lower storey of the upper horizon. Gastropods of the species *Littorina sitchana* and *Gollisella cassis* are encountered in the lower part of the upper horizon and in the upper part of the middle horizon.

In the middle horizon of the littoral zone, in addition to *Collisella cassis* and *Littorina sitchana* which form a continuous mass on individual boulders and rocks, we encounter *Mytilus edulis, Pagurus hirsutiusculus* and *P. middendorffii* .

Balanus cariosus is a characteristic representative of the lower storey of the middle horizon of the littoral zone. Here, this species forms colonies in a very wide strip, covering nearly the entire littoral zone, even in the places with strong surf. Gur'yanova (1935) notes that *B. cariosus* readily and abundantly colonizes the most surf-exposed places on the Commander Isls, and it predominates in the littoral zone, forming the main background of the latter with its vast colonies.

The population of the lower horizon of the littoral zone is highly diverse. Numerous accumulations of amphipods are encountered under rocks and on thalluses of algae. Amphipoda are encountered throughout the third horizon and in the lower storey of the middle horizon.

Birds are an inherent component of the littoral biocoenosis. In the tidal zone during low tide, one can encounter, in addition to the typically littoral sea birds,

various shore-birds (especially sandpipers and turnstones) and birds of the sparrow family (snow buntings, Lapland buntings, white wagtails). The Arctic fox (*Alopex lagopus*) and Norway rats (*Rattus norvegicus*) are encountered frequently. Of the sea mammals, fur seals (*Callorhinus ursinus*), sea-otters (*Enhydra lutris*) and Steller's sea-lions are encountered in the littoral zone.

Material and Method of Study

The material for this study was collected by us on Bering Is. in 1962-1964.

During this period, 1529 specimens of vertebrates belonging to 56 species, 16 orders and 3 classes were examined by Acad. K.I. Skryabin's method of complete helminthological dissection. Another 3465 specimens of littoral invertebrates were also dissected (table 1).

This particular paper deals with the material concerning only 9 species of helminths, the larval stages of which were found in invertebrates, and the adult forms in birds and mammals. The larvae of the parasites were found in 10 species of invertebrates belonging to 3 classes and 6 orders.

The trematode worms extracted from the animals were fixed and preserved in 70% alchohol, and the nematodes in Barbagallo fluid. In some cases, the latter were fixed with hot alcohol, and preserved in Barbagallo fluid.

The lab processing of the helminth collection was carried out in the helminthological lab at the Zoology Department of the Soil Biology Faculty of the Far Eastern State University. The morphology and anatomy of the helminths were studied on whole-mount specimens prepared by the standard method. Whole-mount microscopic specimens were prepared in different ways, depending on which medium the subject was embedded in. Canadian balsam is usually used as a medium for trematode worms, and a mixture of glycerin and lactic acid in equal portions is used for nematodes.

The trematodes were stained prior to embedment in Canadian balsam. They were stained with aluminous carmine, and then differentiated in a mixture of acetic acid and 70% alcohol. After these manipulations, they were passed through alcohols of increasing strength. The worms were clarified in xylene.

Table 1. Number of invertebrates dissected and infested with helminth larvae

Host	Dissected	Infested	%
Phylum ANNELIDES			
Class Polychaeta			
Order Phyllodocemorpha			
Harmothoe imbricata L.	1	-	-
Order Nereimorpha			
Nereis vexillosa Grude	10	-	-
Class Sipunculida			
Physocosoma japonica (Montagu)	5	-	-
Phylum ARTHROPODA			
Class Crustacea			
Order Cirripedia			
Balanus cariosus (Pallus)	497	361	72.6
Order Isopoda			
Idotea ochotensis Brandt	24	-	-
Order Amphipoda			
Orchestia ochotensis Brandt	550	550	100.0
Anisogammarus locustoides (Brandt)	188	20	10.6
Parhyale zibellinia Derzhavin	153	-	-
Echinogammarus atchensis (Brandt)	66	-	-
Order Mysidacea			
Archaeomysis grebnitzkii Czerniavsky	63	-	-
Order Decapoda			
Pagurus hirsutiusculus (Dana)	630	175	27.7
Pagurus middendorffii Brandt	227	46	20.2
Hapalogaster grebnitzkii Schalf	3	-	-
Telmessus cheiragonus (Tilesius)	100	-	-
Phylum MOLLUSCA			
Class Gastropoda			
Order Diotocardia			
Collisella cassis (Eschscholtz)	305	151	49.5

(table 1 continued)

Host	Dissected	Infested	%
Order Monotocardia			
Epheria porrecta (Carpenter)	40	-	-
Littorina sitchana Phillippi	279	97	34.7
Littorina kurila Middendorff	11	-	-
Littorina squalida Broderik et Sowerby	10	-	-
Nucella lima (Martyn)	115	54	46.9
Buccinum baeri (Middendorff)	76	37	46.9
Class Bivalvia Order Dysodonta			
Mytilus edulis L.	102	92	90.1
Modiolus modiolus (L.)	3	-	-
Phylum ECHINODERMATA Class Asteroidea Order Forcipulata			
Leptasterias camtschatica (Brandt)	2	-	-
Order Camarodonta			
Strongylocentrotus polyacanthus Agass. et Clark	5	-	-
Total	3465	1583	45.3

The embedment of nematodes in a mixture of equal portions of glycerin and lactic acid called for fewer manipulations. The parasites were simply transferred from the fluid in which they were kept to the above-mentioned clarifying mixture.

When it was necessary to study the parasites in greater detail, we resorted to microtomy. For thin sections (usually about 6 μ), the specimen was subjected to complex treatment involving embedment in paraffin and cutting with a microtome.

When examining the helminth fauna of invertebrates, the age of the latter was determined just before dissection (by the annuli on the shell in mollusks, and on the carapace in *Balanus*).

Dissection of the invertebrates was carried out with the help of a compressorium. After the subject was examined under a compressorium, the slides were washed off, and the washings examined under a binocular lens. The parasites encountered were removed from the host with the help of two preparation needles.

The anatomical and morphological characters of the metacercariae extracted from the mollusks and crustaceans were studied mainly on living material. For this, they had to be extracted from the cysts. The method of extracting the metacercariae from the cysts was the same as the one used in this case by A.V. Uspenskaya (1963), i.e. cysts with metacercariae were placed in a drop of seawater on a slide; the excess water was suctioned off with a pipette, and the cysts were dried slightly; after that, the cysts were pierced [once] with very sharp preparation needles, and then placed in a drop of seawater. If the encysted metacercariae were alive, they easily came out through the rupture. In the case where the encysted metacercariae showed no signs of life, they were easily extracted by simply applying pressure [to the cysts] with a preparation needle.

The curled up nematode larvae were fixed with hot alcohol, which straightened them out.

The parasites were measured in fixed material. The drawings were carried out with the help of a drawing device installed on a MBI-3 microscope.

TAXONOMIC REVIEW OF THE HELMITH FAUNA FOUND IN LITTORAL ANIMALS

Class T r e m a t o d a Rudolphi, 1808
Family Echinostomatidae Dietz, 1909
Genus *Himasthla* Dietz, 1909

Himasthla militaris (Rudolphi, 1802)
(Fig. 1)

We encountered metacercariae of *H. militaris* in 97 of the 279 examined *Littorina sitchana*, in 151 of 305 *Collisella cassis*, in 37 of 76 *Buccinum baeri*, and in 41 of 102 *Mytilus edulis*. The intensity of infestation was equal to 1-103 specimens. The parasites were localized in the liver, sexual glands and muscle tissue.

The species of the metacercariae was established experimentally. Three week-old nestlings of the glaucous-winged gull were fed metacercariae from *L. sitchana*, *C. cassis* and *M. edulis*. In the course of our study of the trematodes extracted from the intestine of the experimental nestlings, we managed to differentiate five age groups of *H. militaris* (Fig. 1).

One of the factors affecting the degree of mollusk infection with metacercariae is their distribution in the littoral zone. Table 2 contains the data on mollusk infection in the different horizons of the tidal zone. The greatest extensity of

infection was observed in the animals inhabiting the upper and middle horizons. The highest degree of infestation in the upper horizon was noted in *C. cassis*, and the lowest in *M. edulis*. In the middle horizon, *C. cassis* was the most infected , and *L. sitchana* the least infected.

An interesting point to note is that, despite the high degree of infestation of both *C. cassis* and *L. sitchana* in the upper horizon, the average number of *H. militaris* per infected host was by no means high here. It was more than twice as high in the animals from the middle horizon of the littoral zone.

Table 2. Infestation of mollusks with metacercariae of the species *Himasthla militaris* in different horizons of the littoral zone

Mollusk	Horizon	Number of animals			Intensity of infestation		
		dissected	infected spec.	infected %	max.	min.	av.
Collisella cassis	Upper	100	74	74.0	7	1	2.0
	Middle	100	73	73.0	92	1	6.9
	Lower	57	-	-	-	-	-
Littorina sitchana	Upper	100	54	54.0	14	1	2.2
	Middle	93	33	35.4	103	1	5.4
Buccinum baeri	Middle	66	36	54.5	7	1	2.1
Mytilus edulis	Upper	100	39	39.0	10	1	2.4

It has already been noted that the supplementary hosts of *H. militaris* include *M. edulis, L. littorea, L. saxatilis, L. obtusata* and the annelid *Nereis diversicolor* (Kulachkova, 1953; Zelikman, 1955; Chubrik, 1957; Timon-David, Rebecq, 1958).

Up to the present time, maritae of *H. militaris* have been recorded in Western Europe and in the Barents and White seas (Belopol'skaya, 1952; Kulachkova, 1953; Rudolphi, 1802) in the turnstone (*Arenaria interpres*), purple sandpiper (*Calidris maritima*), old-world curlew (*Numenius arquata*), and the common eider (*Somateria mollissima*). On the Commander Isls., this parasite has been encountered in the dunlin (*Calidris alpina*), purple sandpiper (*Calidris maritima*), glaucous-winged gull (*Larus glaucescens*), emperor goose (*Anser canagicus*), and the white wagtail (*Motacilla alba*). The parasite was localized in the intestine. The intensity of infestation was equal to 1-70 specimens. The infected birds were caught from February to September during 1962-1963.

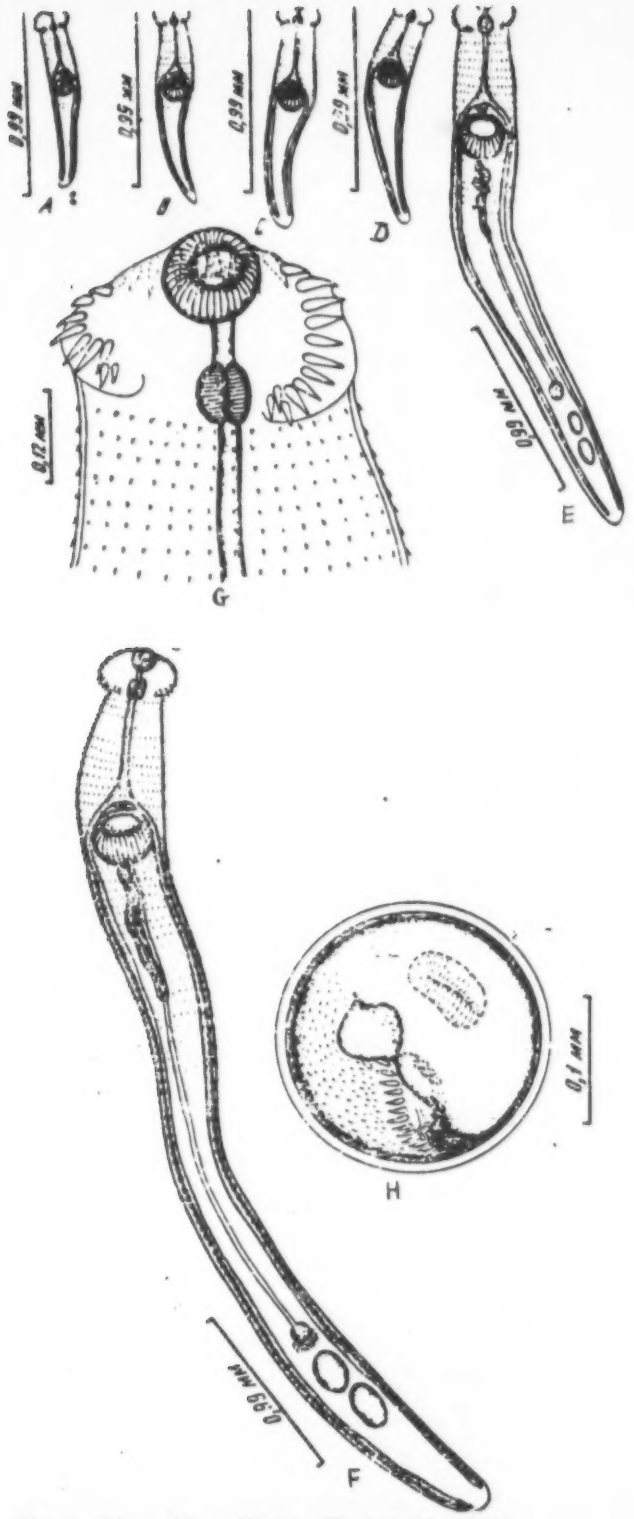

Fig. 1. *Himasthla militaris* (Rudolphi, 1802)

A - a young, 2-day-old individual; B - a 3-day-old individual; C, D - a 4-day-old individual; E - a 6-day-old individual; F - a 10-day-old individual; G - ruffled sucker in immature 10-day-old individual; H - metacercaria from liver of *Collisella cassis*

Family Microphallidae Travassos, 1920
Genus *Microphallus* Ward, 1901

Microphallus pirum (Afanassjew, 1941)
(Fig. 2)

Metacercariae of this species of trematode worms were found in the body cavity of 175 of the 630 dissected *Pagurus hirsutiusculus*, and in 46 of the 227 *P. middendorffii*. The intensity of infestation was equal to 1-12 specimens.

The species of the metacercariae was established experimentally. The experimental animal was an adult puffin (*Lunda cirrhata*)[1] which over a period of 7 days was fed 155 hermit crabs (both species). At the end of the seven days, the puffin was dissected. Its intestine was found to contain 350 adult trematodes which we later identified as *M. pirum*. The anatomical-morphological characteristics of this parasite are as follows. The body is oval, with a slight constriction in the region of the ventral sucker. The cuticle is covered with spinules which disappear in the region of the constriction. The body is 0.59-0.76 mm long, and 0.19-0.39 mm wide in the region of the testes. The subterminal oral sucker is 0.06-0.08 mm in diameter, the prepharynx 0.015-0.035 mm long, the pharynx 0.025-0.040 mm long and 0.020-0.040 mm wide, the esophagus 0.20-0.28 mm long, and the branches of the intestine 0.16-0.25 mm long. The ventral sucker is 0.045-0.065 mm in diameter and occupies a median position. The testes measure 0.06-0.08 mm in diameter, and are arranged symmetrically behind the intestinal branches. The vasa efferentia are indiscernible. The seminal vesicle is located in front of the ventral sucker, and is 0.04-0.05 mm long. The ejaculatory duct is surrounded by the prostate glands. A muscular male papilla 0.03-0.04 mm in diameter lies to the left of the ventral sucker. A spherical ovary 0.04-0.06 mm in diameter lies to the front and slightly to the left of the testis (see Fig. 2 E-G for variations in the position of the sexual glands in relation to the ventral sucker). The oviduct extends from the ovary, and at a distance of 0.015-0.030 mm passes into the ootype which is surrounded by cells of the Mehlis gland. A seminal receptacle is present. The proximal end extends anteriad of the ootype, dorsad of the vitelline duct, bends round the latter and extends posteriorly along the left margin of the right testis, makes several loops, and extends anteriorly. The distal end of the uterus ends in a short metraterm. The vitellariae are gathered in two

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[1] We selected these birds for the experiment on the grounds that they are not carriers of this species of trematode worms. We dissected 109 of these birds, but did not find *M. pirun* in any of them.

groups of small follicles; each group lies behind the testes, slightly overlapping them. A vitelline duct extends from each group of follicles; in the region of the ootype, they fuse into a single short duct which falls into the ootype. The uterus contains 0.020-0.025 x 0.010-0.015 mm eggs.

Table 3. Infestation of hermit crabs with metacercariae of the species *Microphallus pirum* in different horizons of the littoral zone

Host	Horizon	Number of animals			Intensity of infestation		
		dissected	infected spec.	infected %	max.	min.	av.
Pagurus hirsutiusculus	Upper	100	25	25.0	10	1	2.3
	Middle	100	32	32.0	12	1	2.4
	Lower	76	6	7.8	1	1	1.0
Pagurus middendorffii	Lower	72	5	6.9	2	1	1.2

Table 3 contains data on the infestation of hermit crabs in the different horizons of the littoral zone. The crustaceans in the upper and middle horizons were more infected with metacercariae than those in the lower horizon. The maximum intensity of infestation and the average number of parasites per infected host were higher than in the animals inhabiting the middle horizon.

The development cycle of *M. pirum* has been studied by Schiller (1954, 1959). Metacercariae of this helminth were found by him in *Pagurus hirsutiusculus* and *Te[illegible]nessus* sp. from the Aleutian Isls.

A few words now about the taxonomic position of *M. pirum*. V.P. Afanas'yev described this species from the sea-otter (*Enhydra lutris*) and the Arctic fox (*Alopex lagopus*) as a representative of the new genus *Paraheterophyes*. M.M. Belopol'skaya (1952a) proved that the genera *Paraheterophyes* and *Microphallus* were identical, and, as a result, the parasite was given the name *M. pirum* (Afanassjew, 1941), i.e. it retained its species independence. Biguet, Deblock and Capron (1958) give *M. pirum* as a synonym of *M. excellens* (Nicoll, 1907). Belopol'skaya (1963) does not agree with the synonymization of these species, indicating that "the vitellariae in *M. excellens* consist of several large follicles, whereas in *M. pirum* they are formed by very small and numerous follicles... In addition to the morphological differences, the species *M. pirum* and *M. excellens* have different intermediate and supplementary hosts, and their cercariae have a different type of structure" (page 360). In our opinion,

Belopol'skaya presents substantial factual material to corroborate the independence of *M. pirum*.

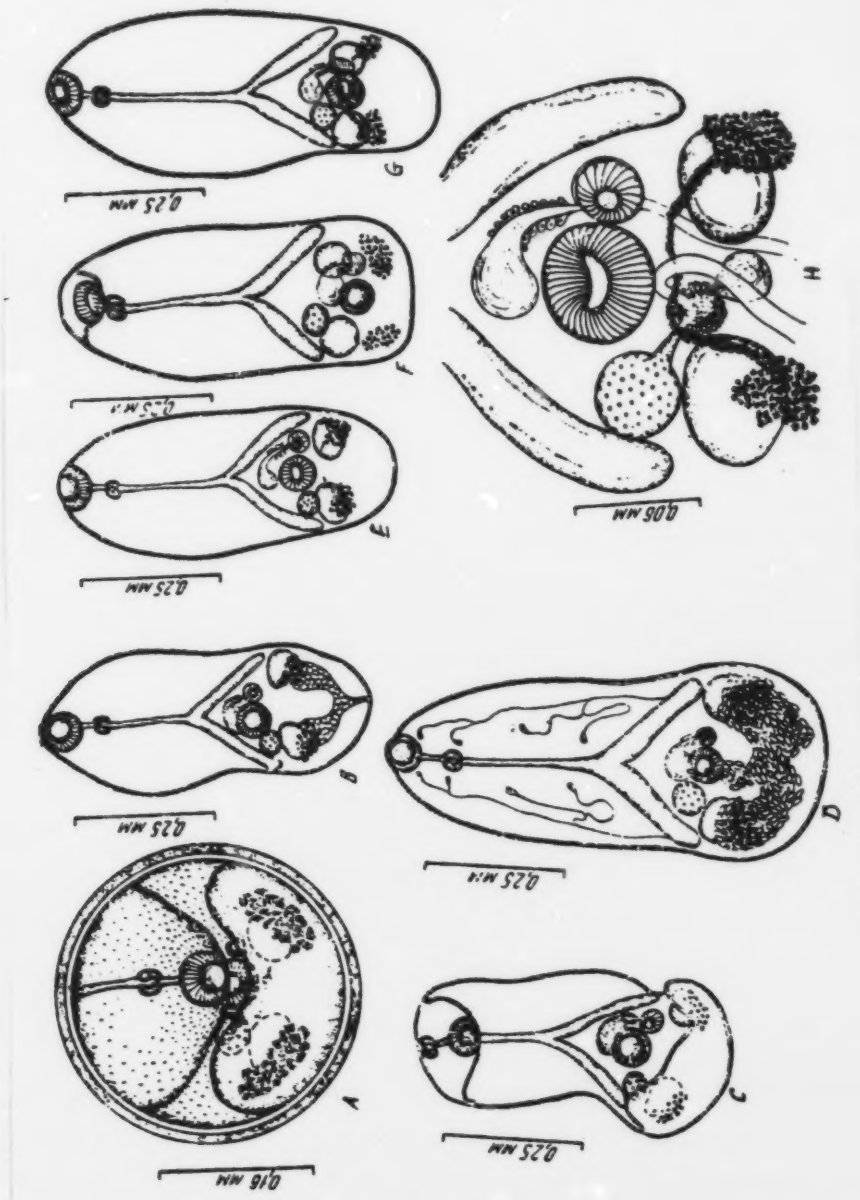

Fig. 2. *Microphallus pirum* (Afanassjew, 1941)

A - metacercaria from *Pagurus middendorffii*, B - the same, not encysted; C - the same, extracted from cyst; D, E, F, G - variations in the body form and size of maritae; H - front and end regions of female and male sex organs

With regard to the distribution of *M. pirum*, we can say that its range is delimited by the coastlines of the Bering Sea and Bering Strait (Rausch, Locker, 1951; Rausch,1953; Schiller, 1954, 1959).

In our material, we have found the definitive hosts of *M. pirum* to be the dunlin (*Calidris alpina*), the purple sandpiper (*Calidris maritima*), the wandering tattler (*Tringa incana*), the glaucous-winged gull (*Larus glaucescens*), and the Arctic fox (*Alopex lagopus*). The helminths were localized in the intestine. The intensity of infestation was 1-1800 worms. The infected animals were caught from February to September during 1962-1963.

Genus *Levinseniella* Stiles et Hassall, 1901

Levinseniella propinqua Jägerskjöld, 1907
(Fig. 3)

The crustaceans *Gammarus locusta* and *G. marinus* can serve as supplementary hosts of *L. propinqua* in the White and Barents seas (Kulachkova, 1953; Uspenskaya, 1963).

We did not find any metacercariae of *L. propinqua* in gammarids inhabiting the littoral zone of Bering Is. However, when a month-old chick that had been fed *Anisogammarus locustoides* and *Echinogammarus atchensis* (332 specimens) over a period of 4 days was dissected, we found one mature trematode. There is no doubt that it belongs to the species *L. propinqua*. The description of it follows.

The body is elongated and expanded posteriorly, 0.85 mm long, with a maximum width of 0.34 mm at the level of the testes. The cuticle is covered with minute spinules which become sparser towards the anterior end of the body, and disappear completely in the region of the ventral sucker. The terminal oral sucker is larger than the ventral one, with a diameter of 0.095 mm. The prepharynx is short, 0.05 mm long. The pharynx is relatively large, with a length of 0.056 mm and width of 0.050 mm. The esophagus is 0.17 mm long. The intestinal branches extend up to the posterior margin of the ventral sucker, measuring 0.32 mm in length. The ventral sucker is 0.6 mm from the anterior end of the body, and its diameter is 0.082 mm. The testes are spherical, 0.089 mm in diameter, and are arranged symmetrically in the posterior part of the body. The seminal vesicle measures 0.084 x 0.04 mm, and lies anteriad and slightly to the right of the vental sucker. The prostate region and prostate glands are well-developed. The ejaculatory duct perforates the male papilla found inside the copulatory organ. The male copulatory organ lies to the left of the

ventral sucker, and has a diameter of 0.09 mm. Inside the copulatory organ, we find a cavity from which four thimble-like pouches extend. The metraterm and ejaculatory duct open into the cavity of the copulatory organ. The genital pore lies to the left of the ventral sucker; it forms a pit with two apertures at the bottom of it, one leading to the double "female pouch", and the other to the male copulatory organ.

The ovary, 0.08 mm in diameter, lies to the right of the ventral sucker, between the right branch of the intestine and the right testis. A short oviduct extends from the ovary, and falls into the ootype which is surrounded by cells of the Mehlis gland. A seminal receptacle is present. The uterus arises from the ootype, extends posteriorly, and occupies a posterior part of the trematode body. The uterus is filled with eggs measuring 0.020-0.022 x 0.010-0.011 mm. The vitellariae are gathered in two groups of follicles, and lie behind the testes. A vitelline duct extends from each group [of follicles]. In the region of the ootype, both vitelline ducts fuse into a single duct which expands and forms a vitelline reservoir. In turn, the vitelline reservoir connects with the ootype by a short duct.

L. propinqua has been recorded in the Barents Sea (Belopol'skaya, 1952a, 1953a) and the White Sea (Kulachkova, 1953; Ginetsinskaya and Naumov, 1958), in the Kaliningrad Region (Golikova, 1959), in the Estonian SSR (Jygis, 1960), in Eastern Siberia (Mamayev, 1959), on the Kurile Isls. (Gubanov, 1952), on the Amur R. (Belopol'skaya, 1963, Juan Sheni, 1962), in the Primorsky Krai (Oshmarin, 1963; Oshmarin and Parukhin, 1963), in Sweden and Central Europe (Jägerskjöld, 1907) in the eastern little stint (*Calidris ruficollis*), dunlin (*C. alpina*), long-toed stint (*C. subminuta*), curlew sandpiper (*C. testacea*), eastern knot (*C. tenuirostris*), sharp-tailed sandpiper (*C. acuminata*), redshank (*Tringa totanus*), greenshank (*T. nebularia*), spotted redshank (*T. erythropus*), Sakhalin sandpiper (*T. guttifer*), wandering tattler (*T. incana*), red-necked phalarope (*Phalaropus lobatus*), snipe (*Gallinago gallinago*), purple sandpiper (*Calidris maritima*), plover (*Charadrius hiaticola*), grey plover (*Squatarola squatarola*), common eider (*Somateria mollisima*), common sandpiper (*Tringa hypoleucos*), oyster-catcher (*Haematopus ostralegus*), shoveller (*Anas clypeata*), water-cock (*Xenus einereus*), ruddy sheldrake (*Todorna ferruginea*), little stint (*Calidris minuta*), turnstone (*Arenaria interpres*), and golden plover (*Charadrius apricarius*).

We came across *L.propinqua* in the Mongolian sand plover (*Charadrius mongolus*), dunlin (*Calidris alpina*), purple sandpiper (*Calidris maritima*), wandering tattler (*Tringa incana*), and fulmar (*Fulmarus glacialis*).

This parasites was localized in the intestine. The intensity of infestation was 1-250 specimens, and the infected birds were caught from February to September during 1962-1964.

Fig. 3. *Levinseniella propinqua* Jägerskjöld, 1907, from a chick intestine:
A - general view; B - starting regions of the female genital system

Genus *Spiculotrema* Belopolskaia, 1949

Spiculotrema litoralis Belopolskaia, 1949

We found metacercariae of *S. litoralis* in 20 of the 188 dissected *Anisogammarus locustoides*. The average intensity of infestation (the number of parasites per infected host) was low, 1.4 specimens. The highest number of metacercariae encountered in one crustacean did not exceed 3.

The species had previously been known from the Kurile Isls. (Iturup Is.) and the Primorsky Krai [Maritime Territory of of the Soviet Far East] (Belopol'skaya, 1949, 1954, 1963a; Oshmarin, 1963; Oshmarin and Parukhin, 1963), where it was found in the turnstone (*Arenaria interpres*), wandering tattler (*Tringa incana*), eastern little stint (*Calidris ruficollis*), and dunlin (*Calidris alpina*).

We encountered this species in the dunlin (*Calidris alpina*), purple sandpiper (*Calidris maritima*), wandering tattler (*Tringa incana*), turnstone (*Arenaria interpres*), harlequin duck (*Histrionicus histrionicus*), and white wagtail (*Motacilla alba*). The parasites were localized in the intestine, the intensity of infestation was 1-900 specimens, and the infected birds were caught from February to September during 1962-1964.

Genus *Maritrema* Nicoll, 1907

Maritrema afannassjewi Belopolskaia, 1952

Metacercariae of this species of trematodes were found in 220 of the 550 analyzed *Orchestia ochotensis*. The intensity of infestation was 1-15 specimens. The cysts were found in the body cavity of the crustaceans, adjacent to the outer wall of the intestine.

Maritae of *M. afanassjewi* had previously been noted in the fox (*Vulpes vulpes*), raccoon-dog (*Nyctereutes procyonoides*), Arctic fox (*Alopex lagopus*), rat (*Rattus norvegicus*) and harlequin duck (*Histrionicus histrionicus*) in Kamchatka (Leonov, Ryzhikov, Tsimbaliuk, Belogrudov, 1963), in Primor'ye (Oshmarin and Parukhin, 1963), and on the Pribylov Isls. (Fay and Williamson, 1962).

In our material, we found the definitive hosts of *M. afanassjewi* to be the American golden plover (*Charadrius dominicus*), Mongolian sand plover (*Charadrius mongolus*), dunlin (*Calidris alpina*), eastern little stint (*Calidris ruficollis*), purple sandpiper (*Calidris maritima*), wandering tattler (*Tringa incana*), turnstone

(*Arenaria interpres*), whimbrel (*Numenius phaeopus*), tufted puffin (*Lunda cirrhata*), pintail (*Anas acuta*), harlequin duck (*Histrionicus histrionicus*), cuckoo (*Cuculus canorus*), white wagtail (*Motacilla alba*), Pechora pipit (*Anthus gustavi*), Lapland bunting (*Calcarius lapponicus*), snow bunting (*Plectrophenax nivalis*), wren (*Troglodytes troglodytes*), Norway rat (*Rattus norvegicus*), and the Arctic fox (*Alopex lagopus*).

This parasite was localized in the intenstine, the intensity of infestation was 1-1800 specimens, and the infected animals were caught from February to September during 1962-1964.

Maritrema arenaria Hadley et Castle, 1940

(Figs. 4, 5, 6)

We encountered encysted metacercariae of *M. arenaria* in 361 of the 497 analyzed *Balanus cariosus*. The cysts were found in the body cavity of the host, adjacent to the outer wall of the intestine. The intensity of infestation was 1-89 specimens.

We noted a gradual decrease in the extensity and intensity of infestation of the host from the upper to the lower horizon (table 4). Infestation increases with the age of the crustaceans (table 5). This applies equally to the extensity and the intensity of infestation.

Table 4. Infestation of *Balanus cariosus* with metacercariae of the species *Maritrema arenaria* in different horizons of the littoral zone

Horizon	No. of animals			Intensity of infestation		
	dissected	infected		min.	max.	average
		spec.	%			
Upper	100	100	100	1	89	15.9
Middle	100	84	84	1	22	5.9
Lower	100	71	71	1	7	2.2

Table 5. Infestation of certain age groups of *Balanus cariousus* with metacercariae of the species *Maritrema arenaria*

Age (years)	No. of animals			Intensity of infestation		
	dissected	infected		min.	max.	average
		spec.	%			
3.5	34	21	61.7	1	11	6.6
4.5	55	47	85.4	1	14	8.9
5.5	53	49	92.4	1	17	9.6

Prior to our investigations, metacercariae of the species *M. arenaria* were found in *Balanus balanoides* by Hadly and Castle (1940). Since we discovered these parasites in a new host and on USSR territory for the first time, we believe that they should be described.

The metacercariae are enclosed in spherical cysts 0.207-0.246 mm in diameter. The wall of the cyst is two-layered, 0.0085-0.0112 mm thick. The body of the metacercaria is 0.46-0.60 mm long, and 0.187-0.200 mm wide. It is oval, and its front end is slightly elongated. The cuticle is covered with spinules. The subterminal oral sucker is 0.035-0.046 mm in diameter. The prepharynx is 0.024-0.027 mm, the esophagus 0.054-0.060 mm, and the intestinal branches 0.160-0.175 mm long. The pharynx measures 0.021-0.022 x 0.019-0.020 mm. The ventral sucker is 0.35-0.04 in diameter. The testes are spherical, and measure 0.058-0.060 mm. The cirrus pouch lies in front of the ventral sucker, and is 0.130-0.137 mm long and 0.037-0.050 mm wide. The seminal vesicle is well-developed. The ejaculatory duct is surrounded by glandular cells. The genital pore lies to the left of the ventral sucker. The ovary, 0.03-0.04 mm in diameter, lies in front of and slightly mediad of the right testis. A short oviduct extends from the ovary, and falls into the ootype. The uterus extends from the ootype, runs posteriorly along the left testis, makes several loops, and then extends diagonally from the right testis to the left one and ends in a muscular metraterm. The latter has the characteristic curve of this species. The vitelline ducts fuse behind and mediad of the ovary.

The fact that these metacercariae belong to the species *M. arenaria* was established experimentally. A week-old nestling of the glaucous-winged gull was fed 220 *Balanus cariosus* over a period of two days. The nestling was dissected on the third day. Its small intestine was found to contain 152 adult trematodes, the description of which follows.

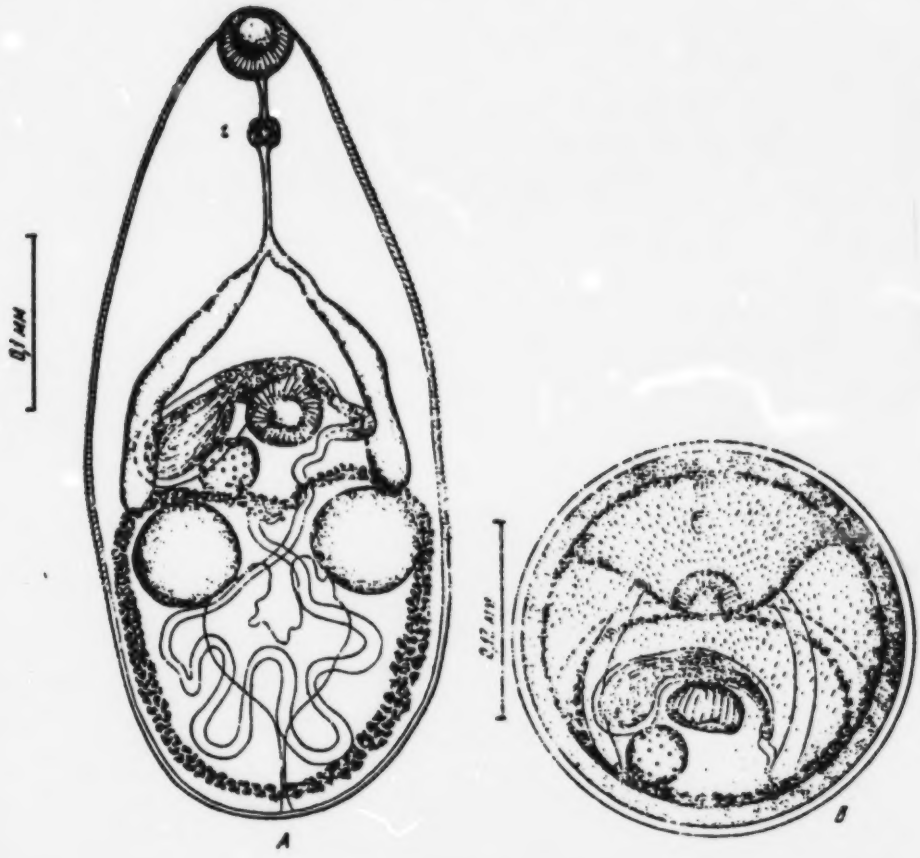

Fig. 4. *Maritrema arenaria* Hadley et Castle, 1940:
A - metacercaria removed from cyst; B - encysted metacercaria from *Balanus cariosus*

The maritae are oval, with a slightly drawn out anterior end. The cuticle is covered with spinules. The worms are 0.55-0.60 mm long, and 0.28-0.36 mm wide in the region of the testes. The subterminal oral sucker is 0.05-0.06 mm in diameter. The prepharynx is 0.025-0.045 mm, the esophagus 0.05-0.08 mm, and the intestinal branches 0.27-0.28 mm long. The pharynx measures 0.020-0.025 x 0.020-0.024 mm. The ventral sucker is 0.05-0.06 mm in diameter, and is located on the median line of the body. The testes are spherical, and measure up to 0.08-0.095 mm in diameter. Their distance from the posterior end is equal to one-third of the length of the body. The cirrus pouch lies in front of the ventral sucker; it is 0.22-0.26 mm long, and 0.045-0.060 mm wide. The seminal vesicle, 0.075-0.090 mm long and 0.045-0.030 mm wide, passes into the ejaculatory duct which is expanded in its middle part. The ejaculatory duct is surrounded by glandular cells. A smooth cirrus falls into the

genital atrium. The latter lies to the left of the ventral sucker, and opens in a genital pore. A round ovary 0.04-0.06 mm in diameter lies between the proximal end of the cirrus pouch, the right testis and the ventral sucker. A short oviduct extends from the ventral margin of the ovary. A seminal receptacle and Laurer's canal extend from the oviduct before it falls into the ootype. The vitelline duct falls directly into the ootype. Emerging from the ootype, the uterus extends in the anterior direction, dorsad of the vitelline duct. Passing the latter, it turns back, bends round the vitelline duct ventrally, and extends toward the posterior end of the body. Here it forms several coils, and extends anteriorly toward the genital atrium. The muscular metraterm has a distinctive left curve. The arrangement of the vitellariae is characteristic of the genus. The yellowish eggs are 0.020-0.028 mm long and 0.011-0.012 mm wide. The excretory vesicle is Y-shaped. The formula of the nephridial cells is (2+2) + (2+2) x 2 = 16.

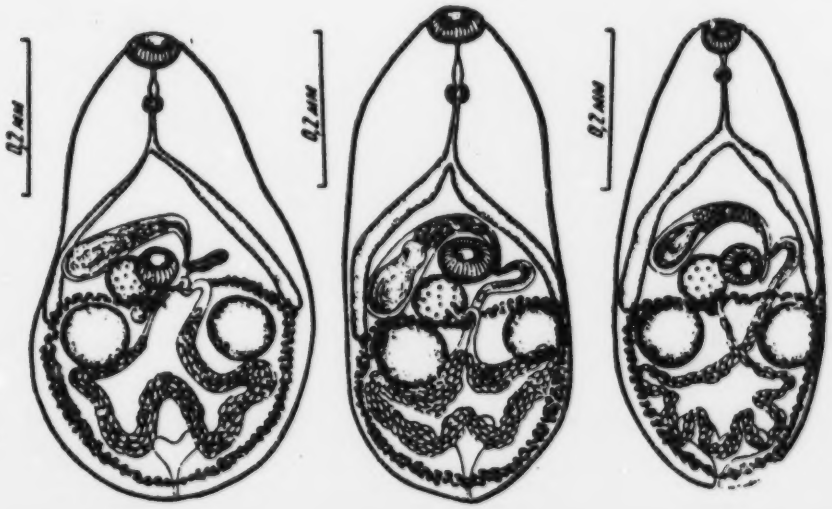

Fig. 5. *Maritrema arenaria* Hadley et Castle, 1940: variations in the body form of maritae from the intestine of an experimentally infected nestling of the glaucous-winged gull

Besides experimental infection of definitive hosts (a nestling of the glaucous-winged gull) with metacercariae of *M. arenaria*, we performed two experiments on the cultivatiion of metacercariae in vitro. We believe that this data should be presented here.

Experiment 1. Seven metacercariae removed from *Balanus cariosus* were placed in seawater diluted 4-fold with well water. Two hours later, 6 metacercariae emerged from the cysts. One ruptured the cyst and died. Two metacercariae died 8 hours later, and the rest 20 hour later. The temperature of the water was about 40°C.

Experiment 2. Fifteen metacercariae were placed in a medium consisting of 16 parts well water and 2 parts pepsin, with a temperature of about 40°C. Four metacercariae emerged from the cysts after 20 min, five after one hour and 45 min, and the rest after 2 hour and 30 min. All of the metacercariae died after 3 hours and 30 min.

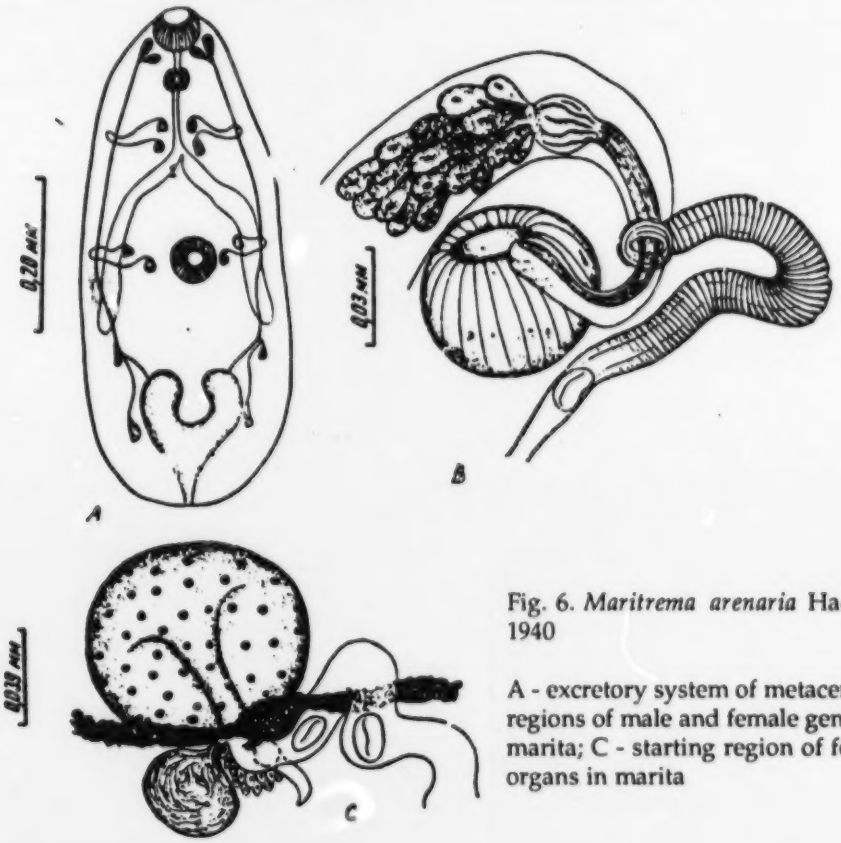

Fig. 6. *Maritrema arenaria* Hadley et Castle, 1940

A - excretory system of metacercaria; B - end regions of male and female genital organs in marita; C - starting region of female genital organs in marita

This species has been described in North America from the turnstone (*Arenaria interpres*). It has been recorded on USSR territory for the first time. Sexually mature trematodes were found in the dunlin (*Calidris alpina*), purple sandpiper (*C. maritima*), and in the wandering tattler (*Tringa incana*). The parasite was localized in the intestine, the intensity of infestatiion was 1-200 specimens, and the infected animals were caught from February to September during 1962-1964.

Genus *Pseudospelotrema* Yamaguti, 1939

Pseudospelotrema japonicum Yamaguti, 1939

As our studies on littoral invertebrates have shown, *Anisogammarus locustoides* is a supplementary host of *P. japonicum*. However, metacercariae are rarely found in this crustacean. Cysts were found in only one of the 188 dissected specimens of *A. locustoides*.

Up to the present time, maritae of this species of trematodes have been recorded in Primor'ye (Belopol'skaya, 1954), along the coast of the Sea of Okhotsk (Belopol'skaya, 1963a), on the Kamchatka Peninsula (Leonov et al., 1963), in Japan (Yamaguti, 1939), and in North America (Ching, 1961) in the wandering tattler (*Tringa incana*), Sakhalin sandpiper (*T. guttifer*), harlequin duck (*Histrionicus histrionicus*), and in the black scoter (*Melanitta nigra*).

On the Commander Isls., this species of helminths has been recorded in the pigeon guillemot (*Cepphus columba*), mallard (*Anas platyrhyncha*), goosander (*Mergus merganser*), and in the harlequin duck.

This parasite was localized in the intestine, the intensity of infestation was 3-100 specimens, and the infected birds were caught from February to July during 1962-1964.

Family Renicolidae Dollfus, 1939

Genus *Renicola* Cohn, 1904

Renicola lari (?) Timon-David, 1933

(Fig. 7)

In littoral mollusks *Mytilus edulis*, *Nucella lima* and *Buccinum baeri*, we came across metacercariae with the following anatomical-morphological characteristics.

The cysts are spherical, 0.27 mm in diameter, with a double membrane (Fig. 7, b). The outer membrane is 0.04-0.05 mm thick, colourless, and is permeated by sparsely scattered impregnations. The inner membrane is dark and much thinner (0.009-0.01 mm) than the outer one. A metacercaria removed from the cyst measures up to 0.28 mm in length and 0.14 mm in width. The cuticle is covered with minute, sparsely scattered spinules. The oral sucker is subterminal. It measures up to 0.06 mm in diameter. The diameter of the ventral sucker is 0.05 mm. The pharynx is spherical, 0.02 mm in diameter.

Upon dissection of an 11-day-old nestling of the glaucous-winged gull which had been fed 67 *M. edulis* over a period of 4 days, we found 14 immature trematodes in the kidneys (Fig. 7, a). They measure up to 0.35-0.41 mm in length and 0.11-0.12 mm in width. The cuticle is covered with minute spinules. The oral sucker is 0.054-0.067 mm in diameter, and the pharynx 0.013-0.021 x 0.021-0.027 mm. The pharynx is followed by a short esophagus up to 0.005-0.06 mm in length. The branches of the intestine extend up to the posterior end of the body; they have thin walls, and because of this are difficult to discern amidst the parenchymatous cells. In some specimens of trematodes, the intestinal branches are completely indiscernible. The ventral sucker is located in the middle of the body, and measures 0.051-0.054 mm in diameter.

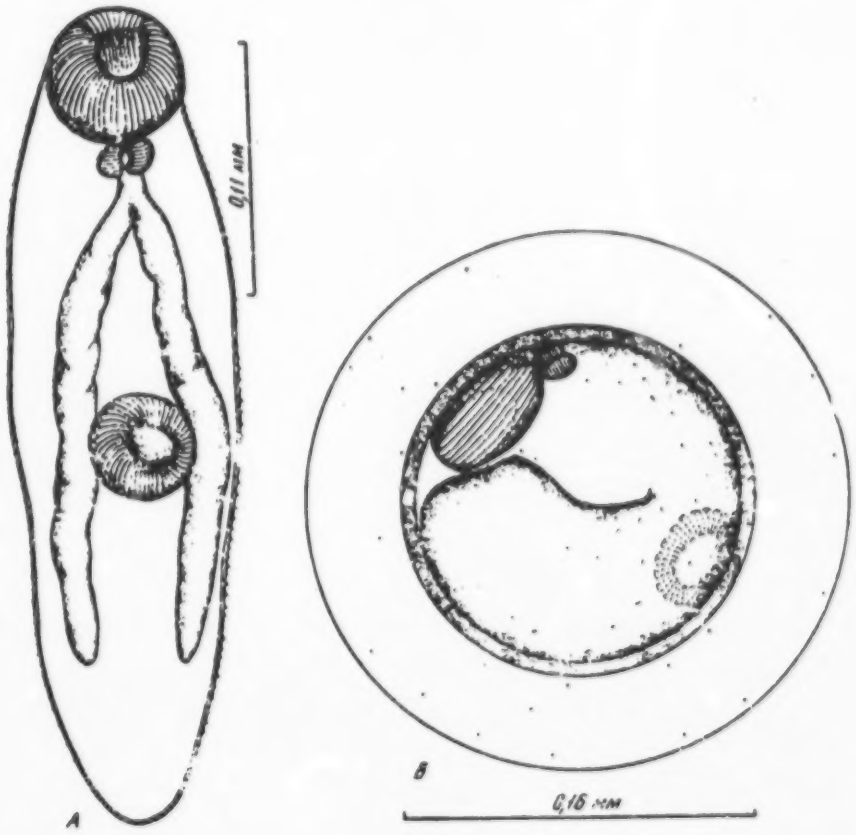

Fig. 7. *Renicola lari* Timon-David, 1933: A - metacercaria; B - encysted metacercaria from *Mytilus edulis*

Table 6. Infestation of mollusks with metacercariae of *Renicola lari* (?)

Mollusk	No. of animals			Intensity of infestation		
	dissected	infected		min.	max.	average
		spec.	%			
Mytilus edulis	102	92	90.1	1	51	9.5
Nucella lima	115	53	46.08	1	1000	32.5
Buccinum baeri	76	16	21.05	1	4	1.3

Proceeding from the above data, it is difficult to say to which of the four *Renicola* species encountered by us in the birds of the Commander Isls. these metacercariae belong. The reason for this is the briefness of the experimental infection of the birds, which did not allow us to obtain mature trematodes. However, considering that *M. edulis* plays no small role in the diet of gulls, we have assigned these metacercariae a priori to the species *R. lari* which is commonly found in these birds on the Commander Isls.

As we have already mentioned, we found metacercariae of this species in three species of mollusks (*Mytilus edulis, Buccinum baeri, Nucella lima*). The first species was collected in the upper horizon, and the other two in the middle horizon. A total of 293 mollusks was dissected, and 161 (54.9%) of them were infected. Of these three species, *M. edulis* displayed the highest degree of infection (table 6).

Nucella lima placed second in the degree of infection. However, the average intensity of infestation in *N. lima* was much higher than in *M. edulis*. Compared with the first two species, *Buccinum baeri* was only slightly infected.

This species of parasite has been recorded in the Barents Sea (Belopol'skaya, 1952), on the central Dnieper R. (Smogorzhevskaya, 1954), in the Rybinsk Reservoir (Shigin, 1954), in the Caspian Sea (Saidov, 1953), in Western Siberia (Bykhovskaya-Pavlovskaya, 1953), in Primor'ye (Belopol'skaya, 1954), on the Kurile Isls. (Gubanov, 1952) and in the southern part of France (Timon-David, 1933, 1955) in the arctic skua (*Stercorarius parasiticus*), blackheaded gull (*Larus ridibundus*), common tern (*Sterna hirundo*), little gull (*Larus minutus*), herring gull (*Larus argentatus*), black tern (*Chlidonias nigra*, black-tailed gull (*Larus crassirostris*), and in the great black-backed gull (*Larus marinus*).

We encountered *R. lari* in the kittiwake (*Rissa tridactyla*), red-legged kittiwake (*Rissa brevirostris*), glaucous-winged gull (*Larus glaucescens*), and in the red-throated loon (*Gavia stellata*).

This parasite was localized in the uriniferous tubules of the kidneys, the intensity of infestation was 1-35 specimens, and the infected birds were caught from February to September during 1962-1963.

Class N e m a t o d a Rudolphi, 1808
Family Acuariidae Seurat, 1913
Genus *Skrjabinocerca* Schikhobalowa, 1930
Skrjabinocerca prima Schikhobalowa, 1930

As our investigations have shown, the intermediate hosts of *S. prima* are crustaceans from the order Amphipoda, *Orchestia ochotensis*. All 550 of the crustaceans dissected by us were found to contain first-, second- and third-instar larvae of the parasite. The intensity of infestation was 1-74 specimens, and the parasite was localized in the body cavity.

Nematodes of this species were first encountered by N.P. Shikhobalova (Schikhobalowa, 1930) in the Corvidae on Sakhalin Is. L.Kh. Gushanskaya (1952) recorded them on the same territory in the hazel hen (*Tetrastes bonasia*), and A.I. Krotov encountered them in the rook (*Corvus frugilegus*) and hazel hen. B.Ye. Kurashvili (1953) encountered *S. prima* in the little stint (*Calidris minuta*) in Georgia; P.G. Oshmarin (1963), P.G. Oshmarin and A.M Parukhin (1963) came across this parasite in the ringed plover (*Charadrius hiaticola*), the dunlin (*Calidris alpina*) and the little ringed plover (*Charadrius dubius*) in Primor'ye, and N.M. Gubanov (1952) found it on the Kurile Isls.

We have encountered this parasite in the guillemot (*Uria aalge*), tufted puffin (*Lunda cirrhata*), Mongolian sand plover (*Charadrius mongolus*), dunlin (*Calidris alpina*), purple sandpiper (*Calidris maritima*), wandering tattler (*Tringa incana*), turnstone (*Arenaria interpres*), red-necked phalarope (*Phalaropus lobatus*), whimbrel (*Numenius phaeopus*), white wagtail (*Motacilla alba*), Pechora pipit (*Anthus gustavi*), Lapland bunting (*Calcarius lapponicus*), snow bunting (*Plectrophenax nivalis*), wren (*Troglodytes troglodytes*), cuckoo (*Cuculus canorus*), and in the Norway rat (*Rattus norvegicus*). *S. prima* was localized in the mucous membrane of the esophagus. In some cases, the intensity of infestation amounted to 125 specimens, averaging up to 9 parasites per square centimetre of the surface of the esophagus. All of the infected birds were caught from May to September during 1962-1964.

BRIEF ANALYSIS OF MATERIAL

Altogether on the Commander Isls., we examined 3465 invertebrates belonging to 25 species, 12 orders, 6 classes and 4 phyla. 45.3% of them were infected with helminths which, at the adult stages, are parasitic on birds and mammals. *Orchestia ochotensis, Mytilus edulis, Balanus cariosus, Collisella cassis, Nucella lima, Buccinum baeri* and *Littorina sitchana* were infected with helminth larvae to the greatest extent. These are the species of animals that dominate in the littoral zone and form the main background of the coenosis. They also predominate in the diet of the vertebrates inhabiting the littoral zone. The wandering tattler of Bering Is. feeds mainly on *Orchestia ochotensis* which abounds in the upper part of the littoral zone. The predominance of these crustaceans in the diet of the wandering tattler resulted in the latter's intense infestation with the nematode *Skrjabinocerca prima* (up to 112 parasites per animal) and *Maritrema afanassjewi* (up to 1500 parasites).

It is with these (above-mentioned) invertebrate animals that the terrestrial vertebrates which are ecologically associated with the seacoast and at times the tundra form the most stable food relations on the island. Even in the Lapland bunting, a typical inhabitant of tundras, we find helminths that develop with the help of littoral invertebrates. Parasitic worms are not a rare occurrence in this animal. The migration of the Lapland bunting, cuckoo, wren and other birds to the littoral zone is determined by the scarcity of food of animal origin in tundra communities, and by the abundance and accessibility of it in the tidal zone. For example, the average biomass of mollusks in the littoral zone of Bering Is. reaches 3 kg/m^2 for *Littorina sitchana*, and 1 kg/m^2 for *Mytilus edulis* (data provided by hydrobiologist T.F. Tarakanova). The average biomass of *Balanus cariosus*, which is part of the *Balanus cariosus+Alaria pylaii* grouping, amounts to more than 5 kg in the middle horizon of the rocky littoral zone near Orlova Kamen'.

The abundance of life in the littoral zone of the Commander Isls. is determined by the fact that the island is surrounded by non-freezing waters with a salinity approximating ocean salinity. Ye.F. Gur'yanova (1935) writes that even in winter, the temperature of the water surface drops to 1.2° only near the shore and after storms; the temperature in the deeper layers reaches 2-2.5° in winter. Therefore, tundra animals are attracted to the littoral zone first of all by the abundance of life, the high biological productivity of the area and by the stability of its communi-

ties. On the other hand, the tundra community, being the youngest one, represents a mobile system; it has fewer species, and is less stable (Naumov, 1963).

Table 7. Infestation of invertebrates with helminth larvae in different horizons of the littoral zone

Horizon	Dissected	Infected	%
Upper	500	292	58.4
Middle	559	258	46.1
Lower	305	82	26.6

In invertebrates characterized by a high degree of infestation with helminth larvae, the parasite fauna proved to be more diverse as well. They were found to contain *Himasthla militaris, Maritrema arenaria, M. afanassjewi, Skrjabinocerca prima* and *Renicola lari* (?) which come from 4 genera, 4 families and 2 classes. In the rest of the invertebrate species found to contain helminths (*Anisogammarus locustoides, Pagurus hirsutiusculus, P. middendorffii*), we came across *Levinseniella propinqua, Microphallus pirum, Pseudospelotrema japonicum* and *Spiculotrema litoralis*. They were far less common in vertebrate animals as well, and they had a smaller range of definitive hosts.

The data in table 7 are quite interesting. They indicate that the degree of infestation with helminths is much higher in invertebrates that inhabit the upper horizon of the littoral zone, than in the same invertebrates from the middle and lower horizons. This distribution of parasites by horizon in the littoral zone is apparently determined by the interrelations of the supplementary and definitive hosts. The mollusks and crustaceans inhabiting the upper part of the littoral zone do not stay underwater as much as those from the lower parts. The latter find themselves in the open air only during the lowest (syzygial) tides. Therefore, the invertebrates inhabiting the middle and particularly the upper horizon naturally come into greater contact with birds and mammals, the definitive hosts of the parasites, than do the invertebrates of the lower horizon. This is also confirmed by the data in table 4. It should be said that the decrease in the extensity of parasitization from the upper to the lower horizon is by no means typical of all invertebrate species. For example, in the hermit crab *Pagurus hirsutiusculus*, which is the supplementary host of *Microphallus pirum*, maximum infestation with metacercariae is noted in the middle horizon of the littoral zone. The fact that the definitive hosts of *M. pirum* include animals that are ecologically associated with the sea expanses (sea-otter) has,

in our opinion, determined the shift of the infestation source to the middle horizon.

Table 8. Confinement of parasites to various groups of hosts

Confinement to groups of hosts	Parasite	Host
Within the same species	*Spiculotrema litoralis*	*Anisogammarus locustoides*
	Maritrema afanassjewi	*Orchestia ochotensis*
	Pseudospelotrema japonicum	*Anisogammarus locustoides*
	Skrjabinocerca prima	*Orchestia ochotensis*
Within the same genus	*Maritrema arenaria*	*Balanus cariosus*
	Levinseniella propinqua	Gammaridae
Within the same order	*Microphallus pirum*	Order Decapoda, *Pagurus hirsutiusculus, Pagurus middendorfii*
Within the same phyllum	*Renicola lari*	Phyllum Mollusca Class Gastropoda *Buccinum baeri, Nucella lima* Class Bivalvia *Mytilus edulis*
	Himasthla militaris	Class Gastropoda *Collisella cassis, Littorina sitchana, Buccinum baeri* Class Bivalvia *Mytilus edulis*

The confinement of parasites to one species of hosts, or to various species (genera, classes, orders) is determined by "the combination of the ecological conditions in which the intermediate or definitive host can exist, and the biological characteristics of the parasite itself" (Uspenskaya, 1963, p. 115). The larvae of *Spiculotrema litoralis, Maritrema afanassjewi, M. arenaria, Levinseniella propinqua, Pseudospelotrema japonicum* and of *Skrjabinocerca prima* are each encountered in one species of invertebrate animals. Therefore, the range of their supplementary or intermediate hosts is very narrow. On the other hand, the range of definitive hosts which the adult forms of these helminths parasitize is broad in the majority of the latter, i.e. it is not limited to one species of animal (table 8).

The species *Himasthla militaris, Microphallus pirum* and *Renicola lari* (?) have 2-3 species as their supplementary hosts. The range of their definitive hosts is even broader, and includes 4-5 species of animals.

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